Vision in hydrothermal vent shrimp

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Bresiliid shrimp from hydrothermal vents on the Mid-Atlantic Ridge have non-imaging eyes adapted for photodetection in light environments of very low intensity. Comparison of retinal structures between both vent shrimp and surface-dwelling shrimp with imaging eyes, and between juvenile and adult vent shrimp, suggests that vent shrimp have evolved from ancestors that lived in a light environment with bright cyclic lighting. Whether the vent shrimp live in swarms and have large dorsal eyes or live in sparse groupings and have large anterior eyes, the basic retinal adaptations are the same across species. Retinal adaptations in adult vent shrimp include the loss of dioptrics, enlargement of both the rhabdomeral segment of the photoreceptors and the light-sensitive rhabdomere therein, attenuation of the arhabdomeral segment of the photoreceptors, reduction of black screening pigment, development of a white diffusing layer behind the photoreceptors, and the loss of rhabdom turnover.

Keywords: black smokers; bresiliid shrimp; retina

1. INTRODUCTION

Knowledge of the existence of hydrothermal vent shrimp at Mid-Atlantic Ridge sites and the recognition that they possessed extraordinary enlarged visual organs are only just over a decade old (e.g. Van Dover *et al.* 1989). Since then, progress has been made in studying the structure (O'Neill *et al.* 1995; Nuckley *et al.* 1996; Kuenzler *et al.* 1997; Lakin *et al.* 1997; Wharton *et al.* 1997) and development (Gaten *et al.* 1998*a*,*b*) of the eyes of a number of species of bresiliid shrimp by using morphological methods, but little is yet known about the visual physiology or behaviour of any of them.

2. MATERIAL AND METHODS

Our descriptions of retinal structure in adult shrimp used specimens collected from the Lucky Strike, Broken Spur, TAG, and Snake Pit hydrothermal vent sites on the Mid-Atlantic Ridge (figure 1) with DSV *Alvin* during R/V *Atlantis II* cruise 129-6/7. Some specimens were examined and dissected in the living state. Some were collected and fixed at depth; others were brought live to the surface and fixed in daylight. Shrimp were fixed either in a buffered double-aldehyde solution, post-fixed in osmium tetroxide and embedded in Epon–Araldite for subsequent examination with light and electron microscopy, or in buffered paraformaldehyde and quick-frozen for subsequent immunocytochemistry. The following species were collected and preserved: *Alvinocaris markensis*, *Chorocaris chacei*, *Chorocaris fortunata*, ?*Chorocaris* (Broken Spur), *Rimicaris aurantiaca*, and *Rimicaris exoculata*. ?*Chorocaris* (Broken Spur) may be identical to *Chorocaris fortunata*. A related species of surface-dwelling shrimp, *Palaemonetes vulgaris*, was subsequently collected, fixed, and analysed for comparison.

3. RESULTS

(a) *Retinal structure*

The two *Rimicaris* species both live in swarms where the front of the animal is likely to be hidden beneath a neighbour, and both species have dorsal, rather than anterior, eyes. By contrast, *A. markensis* and the two (or three) *Chorocaris* species examined live singly or in loose aggregates where the front of the animal is not likely to be masked, and all have anterior eyes. Despite the two different locations of the eyes, the basic cellular arrangement of all the retinas is remarkably similar (figure 2). The eyes are covered by a smooth, transparent, cornea. Inside that, there is a corneal epidermis, sometimes with cone cells, but there are no cuticular cones or any traces of dioptric structures at all. Next comes what could be described as a solid wall of light-sensitive, microvillar rhabdom consisting of 3000–3500 photoreceptors. In each photoreceptor, the rhabdomere fills the cytoplasm of the distal rhabdomeral segment, achieving a volume density of 75–85%. Adjacent photoreceptors abut each other with only the thinnest sheets of white, diffusing, cell processes interposed. Proximally, the arhabdomeral segment continues from the base of the rhabdomeral segment as a very thin cylinder, no wider than the axon that connects to the brain. Near the inner margin of the retina, the arhabdomeral segment swells around the photoreceptor nucleus with the perikaryon, comprising a spherical shell only a few micrometres thick. Beneath the nucleus, the distal end of the axon is filled with black screening pigment granules, which appear to be trapped beneath the nucleus and thereby kept out of the rest of the retina. Proximally, the thin interposed sheets of white diffusing cells expand to form a thick white diffusing layer beneath the rhabdomeral segments. This layer gives
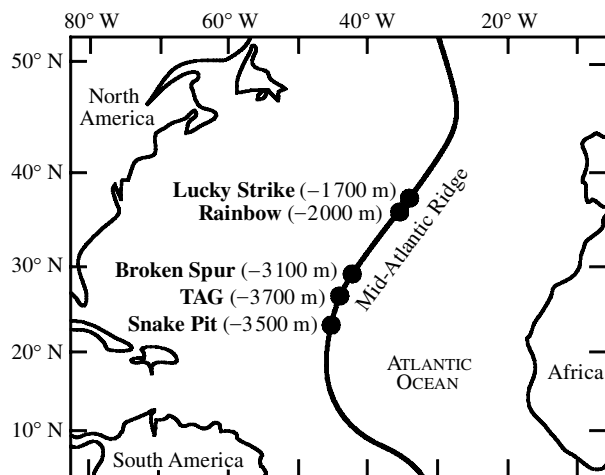
Figure 1. Map showing the location of some hydrothermal vent sites on the Mid-Atlantic Ridge where bresiliid shrimp have been collected for study. The numbers in parentheses give the depths of the vent sites below the surface in metres.

the eyes their white, actually pink, colour and provides an increase in quantum catch as any unabsorbed incoming light is scattered back into the rhabdom. Along the inner edge of the white diffusing cell screen, there are scattered small, black, ellipsoidal screening pigment cells. Thus, the retina appears optimized for light detection at the expense of pattern vision. Note that there are two exceptions to the above summary among the species we have examined: *A. markensis* has lost its photoreceptors in the adult and appears to be blind; and *C. chacei* seems to have a space between the corneal epidermis and the rhabdomeral segments of the photoreceptors.

(b) *Comparison with* Palaemonetes *retina*

Figure 2 also shows the basic retinal structure of the compound eye of *P. vulgaris* for comparison. This anterior, stalked eye is designed for pattern vision both during the day when it functions as an apposition eye and at night when it functions as a quite sensitive superposition eye. During the day, quadripartite cuticular cones gather light for a tight cylinder of microvillar rhabdom, and each of the ommatidia is isolated from its neighbours by a combination of screening pigment cells and reflective interstitial cells. Except for cone cells, which are present in *R. exoculata* but absent from the other hydrothermal vent species, all the cell types in the *P. vulgaris* retina are found in the bresiliid species studied and are found in about the same numbers (e.g. 3100–3800 ommatidia in each wing of *R. exoculata* compared with 3600 in one eye of *P. pugio* or 2800 in one eye of *P. vulgaris*). Furthermore, both *P. vulgaris* and *R. exoculata* appear to use histamine as the neurotransmitter for their photoreceptors (Curra *et al.* 1996). If one takes *P. vulgaris* or a similar surface caridean shrimp as an ancestor of the bresiliid shrimp at hydrothermal vents, then the following changes in retina structure have occurred as these bresiliid shrimp have adapted to the visual environment of the hydrothermal vents:

(i)   the dioptric apparatus has disappeared, trading pattern vision for increased sensitivity;

(ii) the number of photoreceptors has stayed the same, but each has enlarged its rhabdomeral segment and attenuated its arhabdomeral segment, thereby emphasizing absolute sensitivity;

(iii) the volume density of rhabdom, both in the retina overall and in the rhabdomeral segment of the photoreceptors has increased from *ca*. 10–15% to 75–85%, again increasing the absolute sensitivity;

(iv) all morphological evidence of rhabdom turnover has disappeared, and there is no room in either the rhabdomeral or arhabdomeral cytoplasm for significant numbers of multivesicular bodies or other secondary lysosomes;

(v)   the screening pigment in photoreceptors and screening pigment cells which makes the eye of *P. vulgaris* black has been reduced in amount and moved to the inner surface of the retina;

(vi) the interstitial cells separating the ommatidia have enlarged to form a white diffusing screen that increases the sensitivity of the eye and gives it a light colour.

All these changes appear to be adaptations consistent with moving from a visual environment having bright cyclic lighting to one with very dim continuous illumination.

4. DISCUSSION

(a) *Light environment at hydrothermal vents*

We have suggested that the principal source of light at hydrothermal vents could be black-body radiation from the jets of hot vent water escaping the black smoker chimneys on whose sides the shrimp live. Recent spectral measurements (Van Dover *et al.* 1996) of light emitted at the throats of black smoker chimneys are consistent with black-body radiation and suggest that there is an additional mechanism producing light in the green portion of the spectrum, possibly sonoluminescence. The visual pigment of the photoreceptors of *R. exoculata*, for example, is maximally sensitive to green light (Van Dover *et al.* 1989). The intensity, however, of all light at hydrothermal vents is very low, and we determined that it is below the threshold of well-dark-adapted human observers inside DSV *Alvin* (O'Neill *et al.* 1995). Recent studies of *R. exoculata* collected from the Lucky Strike and Rainbow sites suggest that the lights of submersibles are bright enough to cause severe damage to the eyes of the bresiliid shrimp that live there (Herring *et al.* 1999). This may explain our inability to measure any physiological responses to light in collected live specimens of *R. exoculata*, *R. aurantiaca*, or *C. chacei*.

(b) *Evolution and development of hydrothermal vent shrimp*

Recent studies (Gaten *et al.* 1998a,b) of juvenile shrimp collected by trawling above hydrothermal vent sites on the Mid-Atlantic Ridge provide very interesting insights into the possible ancestors of bresiliid vent shrimp. The retinal structure of juvenile vent shrimp resembles much more closely that of the imaging eyes of surface-dwelling species (e.g. figure 2*c*) than it does the retinal structure of adult vent shrimp (e.g. figure 2*b*). In
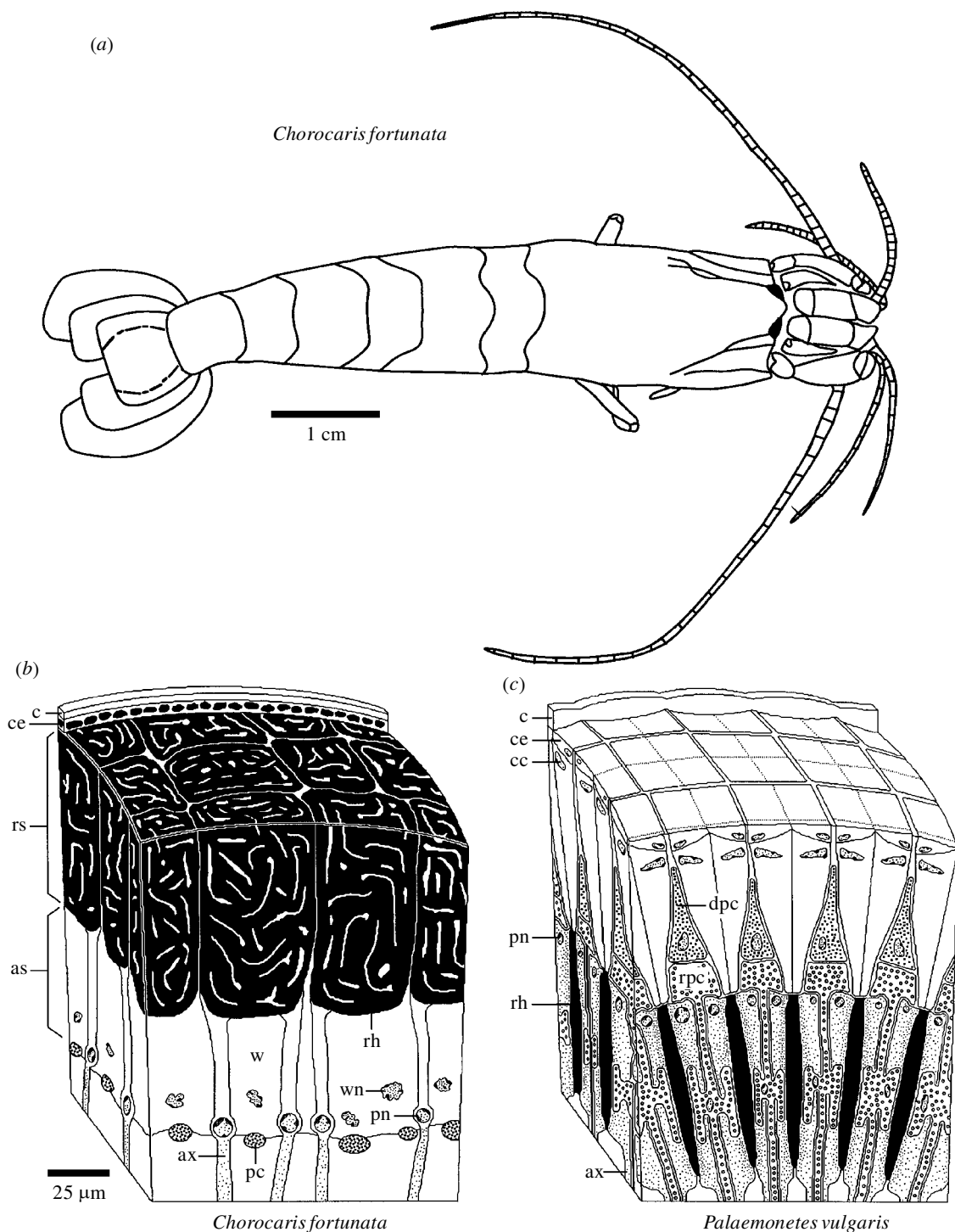
Figure 2. Drawing of a representative bresiliid shrimp with anterior eyes (*a*) and two drawings of retinal structure. (*b*) Cellular arrangement typical of the retinas of hydrothermal vent shrimp. Note the absence of dioptrics and the very large amount of rhabdom shown in black. This retina is adapted for photodetection in very dim light. (*c*) Cellular arrangement typical of surface-dwelling shrimp. Note the presence of square quadripartite lenses that funnel light into the rhabdoms (shown in black) during the day and reflect light into them at night. As drawn, this retina is adapted for pattern vision in daylight. The scale bar in (*b*) is approximate for *C. fortunata*; the drawing in (*c*) is not to the same scale. as, arhabdomeral segment; ax, photoreceptor axon; c, cornea; cc, cone cell; ce, corneal epidermis; dpc, distal pigment cell; pc, screening pigment cell; pn, photoreceptor nucleus; rh, rhabdom; rpc, reflecting pigment cell; rs, rhabdomeral segment; w, white diffusing cell; wn, nucleus of white diffusing cell.

some cases, the transition from an imaging retina to a non-imaging retina can be observed within one eye (Gaten *et al.* 1998*a*). Moreover, in the photoreceptors of juvenile bresiliid shrimp there is ultrastructural evidence of rhabdom turnover in the form of multivesicular and lamellar bodies. Taken together, these data suggest that

vent shrimp have evolved from ancestors that lived in a visual environment bright enough for them to use pattern vision, since the juveniles still show this kind of retinal structure, and that the ancestral environment had cyclic lighting, since the juveniles still show evidence of rhabdom turnover and animals living in

constant light environments typically do not (see O'Neill *et al.* 1995).

One further point is suggested by comparison of the retinal structure of juvenile and adult bresiliid shrimp. As the retina matures from an imaging-type structure to a non-imaging-type structure, the geometrically packed, well-organized microvillar structure of external rhabdom produced by the interleaved microvilli of the multiple photoreceptors in an ommatidium gives way to a preponderance of internal rhabdom formed from microvilli of a single photoreceptor. In surface-dwelling invertebrates with photoreceptors adapted for dim light, such as *Limulus polyphemus*, the microvilli of this internal rhabdom are often not very well organized or geometrically packed (Chamberlain & Barlow 1984). Thus, although some of the seeming disorganization in the ultrastructure of the rhabdom of adult bresiliid shrimp is almost certainly due to factors such as light damage (Herring *et al.* 1999) or other complications of changing chemistry, pressure, and temperature, some loss of geometrical packing may simply be due to the tremendous hypertrophy and internalization of the rhabdomere as the volume density of the microvillar array increases during maturation.

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